Journal of Forestry Research (2013) 24(1): 109–114
DOI 10.1007/s11676-013-0330-4

REVIEW ARTICLE

Ecological effects of atmospheric nitrogen deposition on soil enzyme activity

WANG Cong-yan • Lv Yan-na • LIU Xue-yan Liu • WANG Lei

Received: 2011-09-01; Accepted: 2012-04-04

Abstract: The continuing increase in human activities is causing global changes such as increased deposition of atmospheric nitrogen. There is considerable interest in understanding the effects of increasing atmospheric nitrogen deposition on soil enzyme activities, specifically in terms of global nitrogen cycling and its potential future contribution to global climate change. This paper summarizes the ecological effects of atmospheric nitrogen deposition on soil enzyme activities, including size-effects, stage-effects, site-effects, and the effects of different levels and forms of atmospheric nitrogen deposition. We discuss needs for further research on the relationship between atmospheric nitrogen deposition and soil enzymes.

Key words: global change; nitrogen deposition; soil enzyme activities

Introduction

Soil enzymes play a pivotal role in catalyzing reactions associated with soil organic matter decomposition and nutrient cycling in ecosystems (Ge et al. 2010; McGuire et al. 2010). Soil enzyme activities can be proxies for edaphic properties (Li et al. 2006; Ge et al. 2010), the availability of soil substrates for microbial community and plant uptake (Ge et al. 2010; Yan et al. 2011), the degree of soil pollution (Ge et al. 2010), the degree of external interference in soil ecosystems (Ge et al. 2010; Yan et al. 2011), community structure and metabolic activities of soil microorganisms (Ge et al. 2010; Yan et al. 2011), and the rates of microbial decomposition (Moorhead & Sinsabaugh 2000). Therefore, determination of soil enzyme activities is a powerful tool for understanding the biological processes of soil ecosystems (DeForest 2009). In recent years, soil enzyme activity has received increasing attention in pedology research (Saiya-Cork et al. 2002; Sinsabaugh et al. 2002, 2005; Song et al. 2009; Wang et al. 2010, 2011a, b; Guo et al. 2011a, b; Yan et al. 2011).

Continuing increases in human activities in recent decades have induced climate and environment changes on global scales, including elevated atmospheric nitrogen (N) deposition (Galloway et al. 2008). At present, atmospheric N deposition is a major source of anthropogenic N in the ecosystems in Northeastern United States, Europe, and Asia (Galloway et al. 2008). Ecosystems are predicted to receive increasing amounts of reactive N due to expected increases in human activities in coming decades (Galloway et al. 2008; Schlesinger 2009). Ecosystems even in unpopulated areas are subject to anthropogenic N influences via the long distance transport of such pollutants (Wolfe et al. 2006). Elevated atmospheric N deposition is delivered to ecosystems in excess of biological demand and assimilation capability, and might induce N saturation (van den Berg et al. 2011) and lead to multiple impacts on ecosystems (Hu et al. 2010; van den Berg et al. 2011; Wang et al. 2011a). Anthropogenic N deposition has been identified as a major global threat to ecosystem functioning (Clark & Tilman 2008; Armitage et al. 2012). Effects of atmospheric N deposition on soil enzyme activity have stimulated considerable interest in recent years (Saiya-Cork et al. 2002; Sinsabaugh et al. 2002, 2005; Gallo et al. 2004; Song et al. 2009; Hu et al. 2010; Wang et al. 2010, 2011a; Guo et al. 2011a, b) because soil enzymes play primary roles in organic matter decomposition and nutrient cycling (DeForest 2009; Ge et al. 2010), specifically in terms of global N cycling, and this could impact the rates of climate change in future.

We reviewed the ecological effects of atmospheric N deposition on soil enzyme activity, and discussed shortcomings of current research in this field.

Foundation project: This study was supported by the National Natural Science Foundation of China (30970556, 31170386), and Research Foundation for Advanced Talents, Jiangsu University (12JDG086).
The online version is available at http://www.springerlink.com

WANG Cong-yan (✉)[1, 2] • LIU Xue-yan[1] • WANG Lei[1]
[1.] School of Environmental Sciences, Jiangsu University, Zhenjiang 212013, China; [2.] School of Life Sciences, Nantong University, Nantong 226019, China. E-mail address: liuyuexue623@163.com

Lv Yan-na
School of Life Sciences, Nanjing University, Nanjing 210093, China

Corresponding editor: Hu Yanbo

Size-effects of atmospheric N deposition on soil enzyme activities

There is a growing body of evidence that the effects of atmospheric N deposition on soil enzyme activities are inconsistent. Reasons might include difference in forest types, the type and/or the level of N fertilization, and/or the time scale of the studies (Wang et al. 2010). For example, some studies used "N fertilization" methods. Some investigators found neutral effects of atmospheric N deposition on soil enzyme activities, e.g., oxidase (Keeler et al. 2009), β-glucosidase, N-acetyl-glucosaminidase (Bell et al. 2010), laccase (Blackwood et al. 2007; Lauber et al. 2009), cellulase (Andersson et al. 2004), cellobiohydrolase, xylosidase, phenol oxidase, peroxidase (Bell et al. 2010), and phosphatase (Robroek et al. 2009). This might be due to the fact that: (1) there is N saturation for soil microorganisms (Hobbie 2000); (2) other nutrients, such as phosphorus (P), may be more limiting for the metabolic activities of soil microorganisms (Elser et al. 2009); (3) nutrients have a long residence time leading to a delayed response to additional input of exogenous N; (4) rapid removal of the added nutrients via plant uptake, microbial mobilization, or leaching loss (Silvan et al. 2005; Yavitt et al. 2011); and/or (5) the ecosystem might adapt to exogenous N-input due to its higher homeostatic function under external interference (e.g., atmospheric N deposition)(Hobbie & Vitousek 2000).

Other studies found positive effects of atmospheric N deposition on soil enzyme activities, e.g., cellulase (Wang et al. 2010, 2011a; Liu et al. 2011), β-glucosidase, β-glucosaminidase (Iyyemperumal & Shi 2008; Liu et al. 2011), cellobiohydrolase, protease (Iyyemperumal & Shi 2008), chitinase (Liu et al. 2011), peptidase (Saiya-Cork et al. 2002), β-N-acetylglucosaminidase (Green et al. 2006), dehydrogenase (Kang & Lee 2005), phosphatase, urease (Wang et al. 2010, 2011a), and nitrate reductase (Wang et al. 2011a). This might be due to (1) alleviated N limitation on the metabolic activities of soil microorganisms (Sinsabaugh et al. 2002; Wang et al. 2010, 2011a; Guo et al. 2011a, b), (2) elevated N utilization efficiency of soil microorganisms (Agren et al. 2001), (3) exogenous N can accelerate plant productivity (Xia & Wan 2008) as can aboveground forest litter (Liu & Greaver 2010), which increases the amount of carbon (C) for soil microorganisms, and/or (4) exogenous N can induce a priming effect on the metabolic activities of some microbial communities (Wang et al. 2011a).

Others found negative effects of atmospheric N deposition on soil enzymes, e.g., lignin-degrading enzymes (Janssens et al. 2010), phosphatase, urease, glutaminase, arylsulfatase (Kang & Lee 2005), nitrate reductase (Wang et al. 2010), chitinase (Olander & Vitousek 2000), polyphenol oxidase (Gallo et al. 2004), dehydrogenase, protease (Hu et al. 2010), peroxidase, β-glucosidase (DeForest et al. 2004), catalase, oxidase (Song et al. 2009), cellulase (Sinsabaugh et al. 2002), and nitrogenase (Shevtsova & Neuvonen 1997). This may be due to (1) formation of more recalcitrant materials after complexation between N and polyphenols contained in forest litters (Wang et al. 2010, 2011a), (2) inhibition of lignin-degrading enzymes by low molecular N compounds (Janssens et al. 2010), although lignin-degrading fungi grow slowly and are inefficient in their C use and likely to be out-competed by other soil microorganisms when N is in plentiful supply (Janssens et al. 2010), (3) long-term atmospheric N deposition can reduce plant productivity and input of litter into soil ecosystems, thus reducing the amount of C available to soil microorganisms (Compton et al. 2004) and altering the substrate utilization patterns of soil microorganisms (Thirukkumaran & Parkinson 2000; Wang et al. 2011a), and/or (4) atmospheric N deposition alters edaphic properties (Keeler et al. 2009; Guo et al. 2011b; Wang et al. 2011a), for example, nitrogenous fertilizers might bring more H^+ into the soil subsystem and induce deeper acidification (Keeler et al. 2009; Guo et al. 2011b), this might trigger a series of changes, including changes in the rates of synthesis and release of exoenzymes by soil microorganisms, altered stability of exoenzymes, changes in concentrations of inhibitors or activators in soil solutions and effective concentration of the substrate (Dick et al. 2000).

Effects of different levels of atmospheric N deposition on soil enzyme activities

Levels of natural atmospheric N deposition vary by region and deposition in fast-developing regions is generally higher than that in undeveloped regions (Galloway et al. 2008). Over the past decade, ecologists have become increasing interested in the effects of varying levels of atmospheric N deposition on soil enzyme activities. The effects of varying levels of atmospheric N deposition varied by soil enzyme type in N fertilization experiments. In general, low-level N can accelerate enzymatic activities, while high-level N fertilization reduces soil enzyme activities. Wan et al. (2009) reported that low-level N fertilization can reduce the activities of acid phosphatase and urease, while high-level N fertilization accelerates the activities of these enzymes. Liu et al. (2011) found identical results for the effects of atmospheric N deposition in varying quantities on the activities of β-glucosidase, N-acetyl-β-glucosaminidase, chitinase, and cellulase. This indicates the existence of an N critical load in soil ecosystems. Atmospheric N deposition might have positive effects on soil enzyme activities at levels of atmospheric N deposition below critical values but negative effects when the level of N exceeds a critical threshold (i.e., N-saturated) (Johnson et al. 1998). High levels of N deposition have the greatest impact on lignin degrading fungi because they might be inefficient in their C use (slow growth) and might be outcompeted by other microorganisms when N is plentiful (Janssens et al. 2010) or that high concentrations of low-molecular weight N compounds can suppress the synthesis of lignin degrading enzymes (Edwards et al. 2011).

Effects of different forms of atmospheric N deposition on soil enzyme activities

Natural atmospheric N deposition includes inorganic N (e.g., ammonium and nitrate) and organic N (e.g., urea, amino acids,

aliphatic amines, peroxyacyl nitrates, N heterocyclic compounds, alkyl nitrates, and methyl cyanide)(Cornell et al. 2003). Thus, fertilization experiments using a single form of N cannot give a complete picture of the effects of atmospheric N deposition on soil enzyme activities. Further studies, especially field studies, are required to characterize the ecological effects of different forms of atmospheric N deposition on soil enzyme activities for better understanding of the role of atmospheric N deposition on ecosystems. Forms of N deposition have strong effects on soil enzyme activities (Guo et al. 2011b; Wang et al. 2011a). Wang et al. (2011a) found that mixed forms of N (ammonium, nitrate, and urea balanced mix) had significantly stronger effects than single N (ammonium, nitrate, and urea) on the activities of catalase, cellulase, invertase, polyphenol oxidase, nitrate reductase, urease, and acid phosphatase. The activities of invertase, cellulase, cellobiohydrolase, alkaline phosphatase, and catalase under mixed N (ammonium nitrate, urea, and glycine mix with varied ratios) fertilization were higher than those of single inorganic N (ammonium nitrate) fertilization (Guo et al. 2011b). Possible reasons could be (1) the form of N used by microbial decomposers may vary by species, and/or (2) single forms of N fertilization may disturb the balance of oxidized and reduced N and/or inorganic and organic N for the community of soil microorganisms, leading to lower acceleration effects on microbial functioning than induced by a mixed form of N fertilization (Thirukkumaran & Parkinson 2000; Sinsabaugh et al. 2002; Guo et al. 2011b; Wang et al. 2011a). Organic N had a stronger effect than did inorganic N (Thirukkumaran & Parkinson 2000; Wang et al. 2011a), possibly due to more rapid assimilation of organic N by soil microbes (Thirukkumaran & Parkinson 2000; Gallo et al. 2004; Wang et al. 2011a). Another explanation might be that fertilization with more inorganic N caused deeper soil acidification both in field and laboratory conditions and low soil pH values repress soil enzyme activity (Guo et al. 2011a).

Soil enzyme activities responded differently to various mixed N fertilizations. Soil enzymes exhibited highest activities under mixed N fertilization with the ratio of inorganic N (ammonium nitrate) to organic N (urea and glycine balanced mix) at 3:7 (Guo et al. 2011a, b). Mixed N fertilization might have alleviated forest N-limited conditions more effectively, while excessive inorganic N or organic N might have disturbed the balance of N cycling for the metabolic activities of soil microorganisms, and then lowered the stimulatory effects on enzyme activities (Guo et al. 2011a, b). Mixed N fertilization can increase the resistibility of soil microorganisms to fluctuations in pH mediated by exogenous N and decrease the damage caused by reactive oxygen compounds (Guo et al. 2011b).

Stage-effects of atmospheric N deposition on soil enzyme activities

Ecologists are increasingly interested in understanding the stage effects of atmospheric N deposition on soil enzyme activities because these might be long-term continuing processes. There might be differences in microbial communities during the succession of soil microorganisms, and generally the microbial biomass in early succession is dominated by bacteria, whereas fungi predominate in late succession (Jiang et al. 2009). Exogenous N has a positive effect on bacterial biomass and metabolic activity, while having a neutral or negative effect on fungal biomass and metabolic activity in general (Clegg 2006). Therefore, it is not surprising that some studies found positive effects of atmospheric N deposition on soil enzyme activities in the early phase and negative effects in the later phase. Wan et al. (2009) found that invertase activity was reduced in the first two months and accelerated later under N fertilization, meanwhile, the opposite results were found for acid phosphatase. This suggested that there are stage-effects of atmospheric N deposition on soil enzyme activities.

Site-effects of atmospheric N deposition on soil enzyme activity

Differences in forest communities can influence soil microbe communities directly through variations in the type, complexity, and amount of organic matter input into soils. Microbe communities might differ by forest type, e.g., broad-leaved forests are often dominated by bacteria and coniferous forests by fungi (Schimel et al. 2007). Based on such differences, the activities and communities of soil microorganisms might differ in their responses to the deposition of extraneous N in different forest types. Atmospheric N deposition has the capacity to alter plant community composition and diversity because of species differences in resource acquisition, resource-use efficiency, allocation, growth response, and competitive ability (Xia & Wan 2008; Hautier et al. 2009), which then alter the above- and below-ground interactions, and, in turn, affect soil microbial activities and the related soil enzyme activities. Some investigators also attributed site-specific or forest-specific variations in the effects of atmospheric N deposition to variation in soil enzyme activity. For example, in the *Acer saccharum-Tilia americana* ecosystem, oxidative activity was 38% higher in the litter horizon of high-level N treatment plots, relative to ambient plots, while oxidative activity in mineral soils showed little change. While in *A. saccharum-Quercus rubra* and *Q. velutina-Q. alba* ecosystems, oxidative activity declined in both litter (15% and 23%, respectively) and soil (29% and 38%, respectively) in response to high-level N treatment while cellobiohydrolase activity increased 6% and 39% for litter, and 29% and 18% for soil, respectively (Sinsabaugh et al. 2005). Waldrop et al. (2004) found that the highest level of atmospheric N deposition tended to reduce the activity of phenol oxidase and peroxidase in black oak/white oak ecosystems, and, conversely, atmospheric N deposition tended to increase the activity of the two enzymes in sugar maple/red oak and sugar maple/basswood ecosystems. Some studies found that exogenous N generally accelerates phenol oxidase activity in forest litter with high lignin content, while stimulated or had no effect in forest litter with low lignin content. The dichotomy reflects the critical regulatory role of lignin content on the activity of special enzymes under atmospheric N

deposition (Sinsabaugh et al. 2005). Some investigators found that long-term atmospheric N deposition tended to accelerate microbial biomass and enzymatic activities in N-limited ecosystems, but had no significant effects (Chu et al. 2007) or even negative effects in P-limited ecosystems (Johnson et al. 1998). This suggests that P availability may play a key role in controlling microbial metabolism and enzymatic activity under conditions of atmospheric N deposition (Elser et al. 2009). Site-specific or forest-specific variations in the effects of atmospheric N deposition on soil enzyme activities may be attributed to differences between sites or forest types in nutrient availability (Olander & Vitousek 2000; Treseder & Vitousek 2001), litter lignin content (Sinsabaugh et al. 2002), C:N ratios in forest litter and soils (Michel & Matzner 2003), chemical components of forest litter (Shirato & Yokozawa 2006), microbial biomass (Guo et al. 2011b; Wang et al. 2011a), microbial community composition (Schimel et al. 2007), and the sensitivity of microbial communities to atmospheric N deposition (Hobbie 2000; Wang et al. 2011a).

Sigüenza et al. (2006) suggest that changes in soil microbes are a direct consequence of N deposition, but they might also result from changes in the composition of plant communities because plants provide the substrate for growth of soil organisms. Although plant species has a pronounced effect on microbial community structure, this effect may be masked by exogenous high N inputs (>30 kg N ha^{-1} a^{-1})(Zechmeister-Boltenstern et al. 2011). Therefore, investigation of the direct and indirect effects of atmospheric N deposition on soil enzyme activity is urgently needed, especially in field studies.

Summary

In recent years, numerous studies have investigated the ecological effects of atmospheric N deposition on soil enzymes. While, there are some shortcomings of the current research, we offer the following key summary points:

(1) In different ecosystems, there are large differences in N status, rate and duration of atmospheric N deposition, N forms, and/or time scales of studies. Therefore, it is difficult to compare the effects of atmospheric N deposition on different ecosystems under similar conditions.

(2) Numerous studies have determined the effects of gradient N on ecosystems (Sinsabaugh et al. 2002; Green et al. 2006; Wang et al. 2010). However, natural atmospheric N deposition contains various N components (Cornell et al. 2003) and changes in the form of N deposits are expected in the future (Galloway et al. 2008). Thus, a single N fertilization experiment cannot provide a precise reflection of the effects of atmospheric N deposition on soil enzyme activities. Unfortunately, recent research focuses on the monitoring and simulation with gradient N fertilization in laboratory conditions, while neglecting the effects on ecosystems of different forms of N components derived from atmospheric deposition, especially organic N deposition, or mixed N deposition containing various N components.

(3) Atmospheric N deposition into soils follows several pathways, such as wet- or dry- deposition, and plant uptake (Schlesinger 2009). These pathways might cause different effects on soil enzyme activity. In many simulation experiments, nitrogenous fertilizers were directly applied to soils rather than to above-ground plants to investigate the ecological effects of atmospheric N deposition. In contrast, natural atmospheric N first contacts above-ground plants (or litter) from which it reaches the soil.

(4) Nitrogenous fertilizers in most simulation experiments were added in high dosees in one-off or periodic applications to elicit ecosystem responses within short experimental timescales (Armitage et al. 2012). This ignores the fact that the effects of atmospheric N deposition on ecosystems are a long-term continuous process. Silvan et al. (2005) documented in simulated N fertilization experiments that only 15% of added high-pulse N was assimilated into microbial biomass and 15% was emitted in gaseous form, while plants used up to 70% of added N.

(5) With the continuing increase in human activities in recent decades, the changes in climate and environment are being globalized as well as pluralized. Thus, further studies, especially field studies, are required to characterize the synthesized effects of atmospheric N deposition and other components of global climate and environment change on ecosystem functioning.

(6) Soil microorganisms play key roles in decomposition of soil organic matter and nutrient cycling: microbes are sensitive indicators of soil fertility and quality (Ge et al. 2010; McGuire et al. 2010). Thus, it is important to assess the effects of atmospheric N deposition on the metabolic activity and community composition of soil microorganisms, especially the soil microorganisms which take part in N cycling (e.g., N-fixing bacteria, nitrifying bacteria, nitrosifying bacteria, ammonia oxidizing bacteria, and denitrifying bacteria), to forecast the potential effects of atmospheric N deposition on global N cycling in the coming decades.

Acknowledgement

We are grateful to the anonymous referee for his constructive comments that improved this manuscript.

References

Agren G, Bosatta E, Magill AH. 2001. Combining theory and experiment to understand effects of inorganic nitrogen on litter decomposition. *Oecologia*, **128**: 94–98.

Andersson M, Kjøller A, Struwe S. 2004. Microbial enzyme activities in leaf liter, humus and mineral soil layers of European forests. *Soil Biol Biochem*, **36**: 1527–1537.

Armitage HF, Britton AJ, van der Wal R, Pearce ISK, Thompson DBA, Woodin SJ.2012. Nitrogen deposition enhances moss growth, but leads to an overall decline in habitat condition of mountain mosssedge heath. *Global Change Biol*, **18**: 290–300.

Bell TH, Klironomos JN, Henry HAL. 2010. Seasonal responses of extracellular enzyme activity and microbial biomass to warming and nitrogen addition. *Soil Sci Soc Am J*, **74**: 820–828.

Blackwood CB, Waldrop MP, Zak DR, Sinsabaugh RL. 2007. Molecular

analysis of fungal communities and laccase genes in decomposing litter reveals differences among forest types but no impact of nitrogen deposition. *Environ Microbiol*, **9**: 1306–1316.

Chu HY, Lin XG, Fujii T, Morimoto S, Yagi K, Hu J, Zhang JB. 2007. Soil microbial biomass, dehydrogenase activity, bacterial community structure in response to long-term fertilizer management. *Soil Biol Biochem*, **39**: 2971–2976.

Clark CM, Tilman D. 2008. Loss of plant species after chronic low-level nitrogen deposition to prairie grasslands. *Nature*, **451**: 712–715.

Clegg CD. 2006. Impact of cattle grazing and inorganic fertilizer additions to managed grassland on the microbial community composition of soil. *Appl Soil Ecol*, **31**: 73–82.

Compton J, Watrud LS, Porteus LA, DeGrood S. 2004. Response of soil microbial biomass and community composition to chronic nitrogen additions at Harvard forest. *For Ecol Manag*, **196**: 143–158.

Cornell SE, Jickells TD, Cape JN, Rowland AP, Duce RA. 2003. Organic nitrogen deposition on land and coastal environments: a review of methods and data. *Atmos Environ*, **37**: 2173–2191.

DeForest JL. 2009. The influence of time, storage temperature, and substrate age on potential soil enzyme activity in acidic forest soils using MUB-linked substrates and L-DOPA. *Soil Biol Biochem*, **41**: 1180–1186.

DeForest JL, Zaka DR, Pregitzerc KS, Burton AJ. 2004. Atmospheric nitrate deposition and the microbial degradation of cellobiose and vanillin in a northern hardwood forest. *Soil Biol Biochem*, **36**: 965–971.

Dick WA, Cheng L, Wang P. 2000. Soil acid and alkaline phosphatase activity as pH adjustment indicators. *Soil Biol Biochem*, **32**: 1915–1919.

Edwards IP, Zak DR, Kellner H, Eisenlord SD, Pregitzer KS. 2011. Simulated atmospheric N deposition alters fungal community composition and suppresses ligninolytic gene expression in a northern hardwood forest. *PLoS ONE*, **6(6)**: e20421.

Elser JJ, Kyle M, Steger L, Nydick KR, Baron JS. 2009. Nutrient availability and phytoplankton nutrient limitation across a gradient of atmospheric nitrogen deposition. *Ecology*, **90**: 3062–3073.

Gallo M, Amonette R, Lauber C, Sinsabaugh RL, Zak DR. 2004. Microbial community structure and oxidative enzyme activity in nitrogen-amended north temperate forest soils. *Microbial Ecol*, **8**: 218–229.

Galloway JN, Townsend AR, Erisman JW, Bekunda M, Cai Z, Freney JR, Martinelli LA, Seitzinger SP, Sutton MA. 2008. Transformation of the nitrogen cycle: Recent trends, questions, and potential solutions. *Science*, **320**: 889–892.

Ge GF, Li ZJ, Fan FL, Chu GX, Hou ZN, Liang YC. 2010. Soil biological activity and their seasonal variations in response to long-term application of organic and inorganic fertilizers. *Plant Soil*, **326**: 31–44.

Green H, Bengtsson M, Duval X, Pedersenb HL, Hockenhulla J, Larsenc J. 2006. Influence of urea on the cherry leaf spot pathogen, *Blumeriella jaapii*, and on microorganisms in decomposing cherry leaves. *Soil Biol Biochem*, **38**: 2731–2742.

Guo P, Wang CY, Feng XG, Su MF, Zhu WQ, Tian XJ. 2011a. Mixed inorganic and organic nitrogen addition enhanced extracellular enzymatic activities in a subtropical forest soil in East China. *Water Air Soil Poll*, **216**: 229–237.

Guo P, Wang CY, Jia Y, Wang Q, Han GM, Tian XJ. 2011b. Responses of soil microbial biomass and enzymatic activities to fertilizations of mixed inorganic and organic nitrogen at a subtropical forest in East China. *Plant Soil*, **338**: 355−366.

Hautier Y, Niklaus PA, Hector A. 2009. Competition for light causes plant biodiversity loss after eutrophication. *Science*, **324**: 636−638.

Hobbie SE. 2000. Interactions between litter lignin and soil nitrogen availability during leaf litter decomposition in a Hawaiian montane forest. *Ecosystems*, **3**: 484–494.

Hobbie SH, Vitousek PM. 2000. Nutrient limitation of decomposition in Hawaiian forests. *Ecology*, **81**: 1867–1877.

Hu YL, Zeng DH, Liu YX, Zhang YL, Chen ZH, Wang ZQ. 2010. Responses of soil chemical and biological properties to nitrogen addition in a Dahurian larch plantation in Northeast China. *Plant Soil*, **333**: 81–92.

Iyyemperumal K, Shi W. 2008. Soil enzyme activities in two forage systems following application of different rates of swine lagoon effluent or ammonium nitrate. *Appl Soil Ecol*, **38**: 128–136.

Janssens JA, Dieleman W, Luyssaert S, Subke J-A, Reichstein M, Ceulemans R, Ciais P, Dolman AJ, Grace J, Matteucci G, Papale D, Piao SL, Schulze E-D, Tang J, Law BE. 2010. Reduction of forest soil respiration in response to nitrogen deposition. *Nature GeoSci*, **3**: 315–322.

Jiang JP, Xiong YC, Jiang HM, Ye DY, Song YJ, Li FM. 2009. Soil microbial activity during secondary vegetation succession in semiarid abandoned lands of Loess Plateau. *Pedosphere*, **19**: 735–747.

Johnson D, Leake JR, Lee JA, Campbellb CD. 1998. Changes in soil microbial biomass and microbial activities in response to 7 years simulated pollutant nitrogen deposition on a heathland and two grasslands. *Environ Pollut*, **103**: 239–250.

Kang H, Lee D. 2005. Inhibition of extracellular enzyme activities in a forest soil by additions of inorganic nitrogen. *Commun Soil Sci Plant*, **36**: 2129–2135.

Keeler BL, Hobbie SE, Kellogg LE. 2009. Effects of long-term nitrogen addition on microbial enzyme activity in eight forested and grassland sites: implications for litter and soil organic matter decomposition. *Ecosystems*, **12**: 1–15.

Lauber CL, Sinsabaugh RL, Zak DR. 2009. Laccase gene composition and relative abundance in oak forest soil is not affected by short-term nitrogen fertilization. *Microb Ecol*, **57**: 50–57.

Li WH, Zhang CB, Jiang HB, Xin GR, Yang ZY. 2006. Changes in soil microbial community associated with invasion of the exotic weed, *Mikania micrantha* H.B.K. *Plant Soil*, **281**: 309–324.

Liu LL, Greaver TL. 2010. A global perspective on belowground carbon dynamics under nitrogen enrichment. *Ecol Lett*, **13**: 819−828.

Liu YY, Dell E, Yao HY, Rufty T, Shi W. 2011. Microbial and soil properties in bentgrass putting greens: Impacts of nitrogen fertilization rates. *Geoderma*, **162**: 215–221.

McGuire KL, Zak DR, Edwards IP, Blackwood CB, Upchurch R. 2010. Slowed decomposition is biotically mediated in an ectomycorrhizal, tropical rain forest. *Oecologia*, **164**: 785–795.

Michel K, Matzner E. 2003. Response of enzyme activities to nitrogen addition in forest floors of different C-to-N ratios. *Biol Fertil Soils*, **38**: 102–109.

Moorhead DL, Sinsabaugh RL. 2000. Simulated patterns of litter decay predict patterns of extracellular enzyme activities. *Appl Soil Ecol*, **14**: 71–79.

Olander LP, Vitousek PM. 2000. Regulation of soil phosphatase and chitinase activity by N and P availability. *Biogeochemistry*, **49**: 175–190.

Robroek BJM, Adema EB, Venterink HO, Leonardson L, Wassen MJ. 2009. How nitrogen and sulphur addition, and a single drought event affect root phosphatase activity in *Phalaris arundinacea*. *Sci Total Environment*, **407**: 2342–2348.

Saiya-Cork KR, Sinsabaugh RL, Zak DR. 2002. The effects of long term

nitrogen deposition on extracellular enzyme activity in an *Acer saccharum* forest soil. *Soil Biol Biochem*, **34**: 1309–1315.

Schimel J, Balser TC, Wallenstein M. 2007. Microbial stress-response physiology and its implications for ecosystem function. *Ecology*, **88**: 1386–1394.

Schlesinger WH. 2009. On the fate of anthropogenic nitrogen. *Proc Natl Acad Sci USA*, **106**: 203–208.

Shevtsova A, Neuvonen S. 1997. Responses of ground vegetation to prolonged simulated acid rain in sub-arctic pine-birch forest. *Snv Phytol*, **136**: 613–625.

Shirato Y, Yokozawa M. 2006. Acid hydrolysis to partition plant material into decomposable and resistant fractions for use in the Rothamsted carbon model. *Soil Biol Biochem*, **38**: 812–816.

Sigüenza C, Crowley DE, Allen EB. 2006. Soil microorganisms of a native shrub and exotic grasses along a nitrogen deposition gradient in southern California. *Appl Soil Ecol*, **32**: 13–26.

Silvan N, Tuittila E, KitunenV, Vasander H, Laine J. 2005. Nitrate update by *Eriophorum vaginatum* controls N_2O production in a restored peatland. *Soil Biol Biochem*, **37**: 1519–1526.

Sinsabaugh RL, Carreiro MM, Repert DA. 2002. Allocation of extracellular enzymatic activity in relation to litter composition, N deposition, and mass loss. *Biogeochemistry*, **60**: 1–24.

Sinsabaugh RL, Gallo ME, Lauber C, Waldrop MP, Zak DR. 2005. Extracellular enzyme activities and soil organic matter dynamics for northern hardwood forests receiving simulated nitrogen deposition. *Biogeochemistry*, **75**: 201–215.

Song XG, Hu TX, Xian JR, Xiao CL. 2009. Soil enzyme activities and its response to simulated nitrogen deposition in an evergreen broad-leaved forest, southern Sichuan. *Acta Ecol Sin*, **29**: 1234–1240. (In Chinese)

Thirukkumaran CM, Parkinson D. 2000. Microbial respiration, biomass, metabolic quotient and litter decomposition in a lodgepole pine forest floor amended with nitrogen and phosphorous fertilizers. *Soil Biol Biochem*, **32**: 59–66.

Treseder KK, Vitousek PM. 2001. Effects of soil nutrient availability on investment in acquisition of N and P in Hawaiian rain forests. *Ecology*, **82**: 946–954.

van den Berg LJL, Vergeer P, Rich TCG, Smart SM, Guest D, Ashmore MR. 2011. Direct and indirect effects of nitrogen deposition on species composition change in calcareous grasslands. *Global Change Biol*, **17**: 1871–1883.

Waldrop MP, Zak DR, Sinsabaugh RL. 2004. Microbial community response to nitrogen deposition in northern forest ecosystems. *Soil Biol Biochem*, **36**: 1443–1451.

Wan ZM, Song CC, Liu DY. 2009. The enzyme activity of *Calamagrostis angustifolia* litter decomposition affected by exogenous nitrogen input in a freshwater marsh. *Acta Sci Circum*, **29**: 1830−1835. (In Chinese)

Wang CY, Feng XG, Guo P, Han GM, Tian XJ. 2010. Response of degradative enzymes to N fertilization during litter decomposition in a subtropical forest through a microcosm experiment. *Ecol Res*, **25**: 1121−1128.

Wang CY, Han GM, Jia Y, Feng XG, Guo P, Tian XJ. 2011. Response of litter decomposition and related soil enzyme activities to different forms of nitrogen fertilization in a subtropical forest. *Ecol Res*, **26**: 505−513.

Wang CY, Han GM, Jia Y, Feng XG, Tian XJ. 2011b. Insight into the temperature sensitivity of forest litter decomposition and soil enzyme in subtropical forest in China. *J Plant Ecol-UK*, **5**: 279−286.

Wolfe AP, Cooke CA, Hobbs WO. 2006. Are current rates of atmospheric nitrogen deposition influencing lakes in the eastern Canadian arctic? *Arct Antarct Alp Res*, **38**: 465–476.

Xia JY, Wan SQ. 2008. Global response patterns of terrestrial plant species to nitrogen enrichment. *New Phytol*, **179**: 428−439.

Yan RR, Yan YC, Xin XP, Yang GX, Wang X, Zhang BH. 2011. Changes in microorganisms and enzyme activities in soil under different grazing intensities in meadow steppe, Inner Mongolia. *Ecol Environ Sci*, **20**: 259−265. (In Chinese)

Yavitt JB, Harms KE, Garcia MN, Mirabello MJ, Wright SJ. 2011. Soil fertility and fine root dynamics in response to 4 years of nutrient (N, P, K) fertilization in a lowland tropical moist forest, Panama. *Austral Ecol*, **36**: 433−445.

Zechmeister-Boltenstern S, Michel K, Pfeffer M. 2011. Soil microbial community structure in European forests in relation to forest type and atmospheric nitrogen deposition. *Plant Soil*, **343**: 37–50.